FACTORS AFFECTING PREDATION ON COLLEMBOLA BY VARIOUS ARTHROPODS,

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Analyse.

Durant les huit dernières années, nos recherches ont porté sur les prédateurs des Collemboles. Tandis que la plus grande partie de ces études ont été à la base d'autres travaux, certains de nos résultats qui présentent un caractère d'intérêt général sont exposés ci-dessous. L'on remarquera que : partant de trois séries d'expériences se déroulant dans des conditions complètement différentes, l'on aboutit à des résultats qui concordent.

Over the last eight years we have engaged in several series of experiments studying collembolan predators. While much of this study has been in support of other work, some of our results which may be of general interest are reported below. Although three series of studies were involved, run under quite different conditions, the results were very comparable.

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A great deal of work has been done on collembolan predators in recent years. Simons' (1964) excellent work gives a large view and excellent bibliography. Over the last eight years we have engaged in several series of experiments studying collembolan predators. While much of this study has been in support of other work, some of our results which may be of general interest are reported below. Although three series of studies were involved, run under quite different conditions, the results were very comparable.

Methods and Materials.

Two series of experiments were carried on in the Laboratoire Souterrain at Moulis (Ariège, France). The first of these was done in 1962 and involved predation by various species of *Aphaenops* (*Coleoptera* trechini) upon several different genera of collembola. The other series involved a much more detailed analysis of predation by

Scotolemon lespesi (opilionid) and *Lithobius troglodytes* (centipede) upon various species of *Pseudosinella*. All of these experiments were carried on in the underground laboratory and used crystallizing dishes 20 to 30 centimeters in diameters and 10 centimeters high. The bottoms of the dishes were covered with a uniform layer of cave clay and kept moist. In the first series of experiments, each dish was covered with a glass plate, while in the second series cellophane was used to give a tighter seal.

The reamining two series of experiments were carried on at Grinnell. Both used as experimental chambers clear plastic boxes $22 \times 7 \times 6$ centimeters in size. The plastic covers were pierced with two small openings covered with bolting cloth. The bottoms of the containers were covered uniformly with cave clay.

In the first series of experiments, the predation of three species of trechine beetles (*Neophanops tellkampfi, Pseudonopthalmus grandis,* and *Ameroduvalis jeanneli*) upon various species of collembola was studied. These experiments were carried on in a dark artificial cave chamber at 14° centigrade. The second series involved predation of spiders on *Sinella curviseta* and *Folsomia candida,* and these were carried on at room temperature (18°-24° centigrade) under diffuse illumination.

Predation by trechine beetles.

These studies were carried on under varied conditions. In most cases, 1-4 beetles were used and 5-10 prey animals. In all save a few cases only a single prey and a single predator species were used at one time. In an attempt to overcome the problem of differing numbers of predators and prey animals I developed an escape efficiency index for each predator prey interaction. This was done by first finding the average survival time for the prey animal in culture with a given predator. An arbitrary limit of 50 days maximum survival for any individual was set to minimize distortion by single animals. The prey-predator ratio was determined by taking the number of prey present at the start of the experiment and dividing this by the number of predators. The escape index was then derived by dividing the average survival by the prey-predator ratio.

Table 1 shows these various data for the different species interaction studied. It is clear that the escape efficiency differs strikingly among collembolan species but varies much less from predator to predator. The similarity between *Aphaenops* and *Neophanops tellkampfi* predation is surprising in view of the different conditions under which the two sets of data were obtained (see *Methods and Materials*). By comparing cases where the same species of prey has been used, we can arrive at a series of predation efficiency among these trechine beetles as follows :

Neophanops $\simeq$ *Aphaenops* $>$ *Ameroduvalis* $>$ *Pseudonopthalmus.*

TABLE I.

Carnivore species	Prey species	Total number prey A	Number prey at end of experiment B	Number prey ÷ number predators at start C	Average number days escape of prey D	D/C = escape efficiency	Mean escape efficiency
Neaphanops tellkampfi	*Sinella caeca*	20	1	2.25	3.6	1.6	
Pseudoanophtalmus grandis	» »	37	3	3.5	10.0	2.9	2.4
Ameroduvalis jeanneli	» »	30	0	1.4	3.1	2.2	
N. tellkampfi	*S. curviseta*	30	4	2.9	6.8	2.3	2.8
A. jeanneli	» »	25	8	2.3	7.7	3.4	
N. tellkampfi	*S. krekeleri*	5	1	1.0	6.0	6.0	6.1
A. jeanneli	» »	10	5	2.5	15.3	6.1	
N. tellkampfi	*Lepidocyrtus cyaneus*	5	0	1.7	2.0	1.2	
P. grandis	» »	5	0	5.0	5.8	1.2	1.3
A. jeanneli	» »	15	6	2.5	3.3	1.4	
N. tellkampfi	*Folsomia candida*	36	0	3.1	3.1	1.0	
P. grandis	» »	24	1	2.4	3.2	1.3	1.2
A. jeanneli	» »	15	0	2.1	3.4	1.6	
N. tellkampfi	*Onychiurus sp.*	30	0	2.3	3.0	1.3	
P. grandis	» »	10	0	2.5	7.0	2.8	1.4
Aphaenops sp.	» »	30	2	4.2	4.7	1.1	
N. tellkampfi	*Tomocerus minor*	5	2	1.7	19	11.2	
P. grandis	» »	5	2	2.5	20	8.0	11.3
Aphaenops sp.	» »	22	7	2.5	30	12.0	
Aphaenops sp.	*T. problematicus*	22	5	2.2	24	10.9	

Among the collembola the comparitively inactive forms *Onychiurus* and *Folsomia* are relatively inefficient at escape. The repellent blood and autohemmorage of *Onychiurus* do not appear to function against trechines. *Lepidocyrtus* is very inefficient at escape, but this is probably explained by the fact that this species is the only one studied which does not adapt well to the cave conditions under which these experiments were run. It remained inactive, thus becoming easy prey.

The *Tomocerus* species and *S. krekeleri* are more than four times as efficient at escape as the three forms metioned above, while the two species of small *Sinella* were intermediate.

Predation by spiders.

The spiders here studied were obtained in berlese funnels from soil litter. No identification was made, but they were all small forms

ranging from 2-5 mm. in body length. One to three spiders were placed in each container and 20-100 collembola were used at each time. In every case, a mixture of *Folsomia candida* and *S. curviseta* in equal numbers was offered, and the experiments were carried on in the lighted laboratory room. Table 2 summarizes the results of these experiments. It can be seen that the escape efficiencies of both species are much less than those seen in the trechine experiments. In most cases the spiders constructed webs which were quite efficient at catching collembola. *Folsomia* was still more vulnerable than *Sinella* since the large fragile setae (lasiotrichia) in the latter species aided in escaping from these webs, even though their greater activity made them more susceptable of becoming entrapped.

TABLE II.

Spider Predation Efficiency.

Carnivore species	Prey species	Total number prey A	Number prey at end of experiment B	Number prey ÷ number predators at start C	Average number day escape of prey D	D/C = escape efficiency	Number eaten Per spidere
Miscellaneous spiders	*F. candida*	200	71	20	8.3	.42	94
	S. curviseta	200	98	20	11.0	.55	39

Predation by opilionids and chilopods.

The prey in this series of experiments was limited to five french species of the genus *Pseudosinella*. This was the most extensive series of predation experiments we ran, and our primary aim was to see whether or not there was any changes in escape from predation associated with evolutionary cave adaptation.

On predator was placed in each dish and ten collembola were added, five of each of two species. Records of the animals eaten were kept for six weeks after the start of each experiment. The containers were kept in the Moulis cave under the ambient cave conditions. As predators, we used *Scotolemon lespesi* (opilionids) and *Lithobius troglodytes* (chilopods). Three species pairs of collembola were used : *P. decipiens* and *P. subinflata* ; *P. superduodecima* and *P. theodoridesi* ; and *P. subduodecima* and *P. theodoridesi*. In each case, the first species of the pair is presumed to be the troglophile, ambimorph species of the same lineage of the troglomorph, troglobite second species. Each species pair was tested in replicate experiments with opilionids and chilopods, with and without food present.

Food was placed in one spot at the side of the dish and consisted of a small morsel of yeast.

The behavior of the collembola when introduced into these chambers was clearly different from that seen in other comparable chambers. The presence of the predators appeared to affect the animals, as witnessed by the increased tendency to escape from the containers and the greater number of animals found on the sides and top of the containers, as compared to similar containers used in distribution experiments. Animals lost during the period of observation were presumed eaten, since survival experiments showed virtually no natural loss during the first five weeks.

Results and discussion: Chilopod versus opilionid.

The first, clearest, and most surprising conclusion was that the slow, lethargic opilionid, which often seemed not to move from one week to another, was a much more effective carnivore than the active, aggressive chilopod (see Table 3). The trechine predation

TABLE III.

Predation efficiency.

Scotolemon lespesi and *Lithobius troglodytes*.

Carnivore species	Prey species	Total number prey	Number prey at end of experiment	Number prey ÷ number predators at start	Average number days escape of prey	D/C = escape efficiency
Opilionid	*Pseudosinella decipiens*	50	15	10	18.4	1.84
Chilopod	» »	50	37	10	28.7	2.87
Opilionid	*P. subinflata*	50	7	10	14.0	1.40
Chilopod	» »	50	37	10	29.7	2.97
Opilionid	*P. superduodecima*	45	22	10	24.0	2.40
Chilopod	» »	50	35	10	30.2	3.02
Opilionid	*P. theodoridesi*	45	14	10	19.7	1.97
Chilopod	» »	50	19	10	22.3	2.23
Opilionid	*P. subduodecima*	45	12	10	20.8	2.08
Chilopod	» »	40	20	10	25.3	2.53
Opilionid	*P. theodoridesi*	45	15	10	20.5	2.05
Chilopod	» »	40	23	10	25.1	2.51

experiments were run under different conditions, but some reasonable comparisons can be made between these *Pseudosinella* prey animals and the two species of active *Sinella* in the trechine beetle experiments (see Table 1). On this basis it would appear that the opilionids are more efficient than, while the chilopods are on a par

with the trechines. The fact that prey/predator ratios were generally lower in the opilionid and chilopod experiments than in trechine experiments might be distorting this relationship a little. While opilionid predation upon active collembola has been known for some time (Immel, 1954), the efficiency of this feeding is surprising. The opilionids consumed 68 % of the collembola during the course of the experiments while the chilopods consumed only 38 %. In addition, in four cases the opilionids consumed all the collembola whereas the chilopods never did. There was a considerable variation in individual consumption (see Table 4), but this was within clear limits when averages were considered, and there was no overlap in individual specimen average predation between the two species. The mechanism by which opilionids are able to capture the active *Pseudosinella* may be a chemical anesthetic (Juberthie pers. comm.).

TABLE IV.

Predation by individual predators.

Vertical order represents time sequence of experimental series with one day between experiments.

Experiment	A	B	C	D	E	F	G	H	Predator
1	2/8(*)	1/2	4/5	2/3	0/7	1/7	1/1	2/4	*Scololemon lespesi*
2	5/4	2/6	4/4	2/2	4/4	4/5	7/3	4/5	
3	3/3	3/3	5/5	2/5	3/2	1/5			
4	3/2	3/4	5/0	4/4					
5	2/4	1/6							
Average number eaten/expériment	7.2	6.2	8.4	5.8	6.7	8.5	6.0	7.5	
Size predator	2.5 cm	1 cm	2 cm	2.3 cm	2 cm	2 cm	2 cm		
Experiment	A	B	C	D	E	F	G		
1	3/3	0/4	1/3	3/1	1/0	1/1	5/4		*Lithobius troglodytes*
2	0/1	0/0	3/0	2/3	1/3	0/0			
3	3/3	0/1	0/3	5/2	4/0	2/3			
4	1/2	2/3	4/0	2/1	2/2	2/0			
5	5/4	1/7			1/1				
Average number eaten/experiment	5.4	3.8	3.5	4.7	3.0	2.2			

(*)x/y. where x equals the number eaten during the first week of the experiment, and y equals the number eaten during the last five weeks.

Time of eating.

In the majority of cases the heaviest loss of animals occured within the first week of the experiment. 45 % of the animals eaten by the opilionids and 48 % of those eaten by the chilopods were consumed in this period. Studies run on 23 experiments where three

readings were taken during the first week after starting the experiment showed that 2/3 of these animals were eaten in the first three days after transfer. The predators were kept away from the collembola until the latter were apparently normally active so that the shock of transfer could not be the explanation. Part of the explanation for the initial high casualty rate is probably based on hunger and predator activity. In most cases where there is a high initial predation, the predator had consumed most of the previous experiment's animals several weeks before the end of the experiment. In addition to this, it is quite probable that the collembola were sufficiently disoriented by transfer that normal escape mechanisms were not fully active. The change in rate of predation between the first and last weeks cannot be explained merely as a result of change in density of prey animals, since the rates are not proportional. Below, the loss during each of the six weeks of each experiment is given as a percentage of animals existing at the start of that week :

Week	1	2	3	4	5	6
	24 %	12 %	9 %	10 %	12 %	6 %

As can be seen from this data, the percentage is very high the first week, relatively constant from weeks 2 through 5, and drops during the last week.

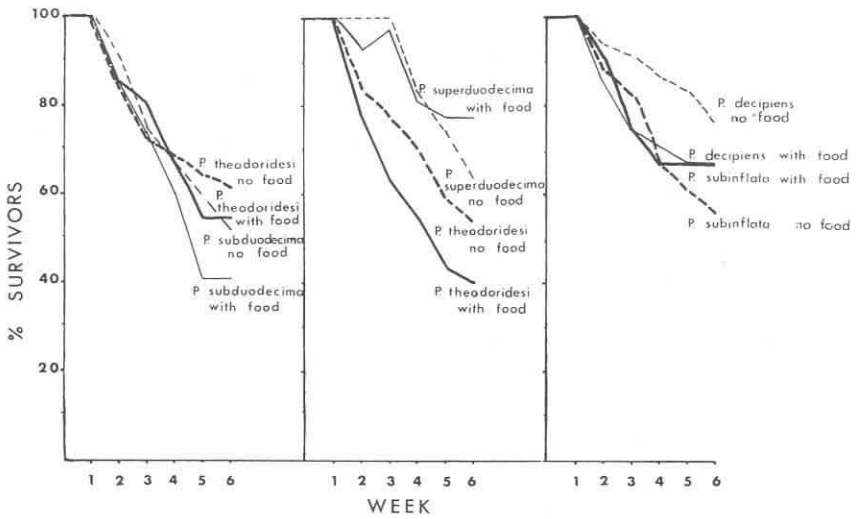
The different species studied show some variation in the proportion of organisms eaten in the first week as opposed to the last five weeks, as shown in the figures below. Only *P. decipiens* shows a clearly greater loss during the first week. In all cases save *decipiens*, the variance is much higher for the last five weeks than the first week.

	% loss (of total)		
1 st week	last 5 wks.	total	species
18	24	43	*P. superduodecima*
21	42	63	*P. subduodecima*
24	35	59	*P. theodoridesi*
28	20	48	*P. decipiens*
29	27	56	*P. subinflata*

Loss rates.

Loss rates can be calculated in many ways but, because of the various factors involved in the first week already discussed, I have considered loss rates after the first week as most important for showing differences among species of prey. Figure 1 shows these rates for the three combinations of species studied under each of the two conditions. With the *P. decipiens - subinflata* cultures, it is clear that only *P. decipiens* is in any way distinguished from the others

under no-food conditions, showing a much better escape under those conditions. In the case of *P. theodoridesi* and *P. subduodecima,* only *P. subduodecima* is distinguished, by a lower escape rate when food is present than when it is absent in experiments, while with *P. theodoridesi* and *P. superduodecima,* the latter species has a consistently better escape than the former. This difference between *P. theodoridesi* and *P. superduodecima* was analyzed statistically, using the Wilcoxon rank test to ascertain the probability of such a separation by chance, and this was less than 1 %. If the troglobitic and troglophilic populations are plotted over each other, it is clear that the former form a homogenous group while the latter are quite varied.



Mean survival after first week under predation by opilionids or chilopods. Three different species pairs tested. Each pair tested with and without food present.

Correlation between losses.

The next question was whether when one species was eaten, this relieved pressure on its paired species or whether an active carnivore tended to eat both species when active and neither when inactive. For this, the various paired results were analyzed using the Spearman's Rho. In the case of *P. decipiens* and *P. subinflata,* there was a positive correlation of .634, significant statistically at the .01 level. The other two species have no significant correlation. Thus, in the case of the first mentioned pair the forms tended to be eaten together, but in both pairs with *P. theodoridesi* the species seemed to go their own separate ways, and there was no connection between heavy predation on one species and another.

Species difference : losses to chilopods and opilionids.

There were striking differences among the various *Pseudosinella* species in regard to predation by opilionids, as compared to chilopods. The figures below show clearly that all species were more heavily affected by opilionids, but the difference was much more striking in the cases of *P. decipiens* and *P. subinflata* than in the other species studied.

% loss in all experiments of each type		
to chilopods	to opilionids	species
24	50	*P. superduodecima*
48	75	*P. subduodecima*
52	68	*P. theodoridesi*
26	70	*P. decipiens*
26	86	*P. subinflata*

General discussion and conclusions.

It is clear that, if we consider predation rates in the form of an adjusted index, there is a remarkable consistency in rates for the same species of prey over a wide variety of predators with an excpetion to this in the spiders. On the other hand, there is a striking difference among groups of collembola. Size and mobility appear to be the most important determinants of escape success among these species. The two relatively immobile forms (*Folsomia* and *Onychiurus*) along with the *Lepidocyrtus,* which are immobilized by the cave conditions of most of these studies, all had low escape efficiencies (1.2-1.4). The three large species (*S. krekeleri, T. minor, T. problematicus*) had high efficiencies (6.1-11.3) and the six small active forms had intermediate values (2.2-2.8). Cave adaptation does not have a consistent or obvious effect on predator escape efficiency. The two highly adapted troglobite *Pseudosinella* species are slightly less efficient at escaping opilionids and chilopods than are their troglophile relatives. On the other hand, the troglobite *T. problematicus* is on a par with the troglophile *T. minor* in escaping from trechine beetles, while *S. krekeleri* is much more efficient than either troglophile *Sinella* species. The last effect seems much more likely to be the result of size difference rather than cave adaptation. In *Pseudosinella,* at least, it does appear that the troglophile forms are more susceptible to predation in the presence of food, while the troglobites show no such tendency. This correlates well with the fact that these forms show a much greater tendency to aggregate around food (Christiansen, 1970).

Spiders are clearly different from the other forms studied in all respects. Generally they appear to be much more efficient predators than chilopods, opilionids or trechines ; however more experiments

would have to be run before any general comparisons could be made.

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Summary.

Species of collembola differ strikingly in their susceptibility to predation. The differences are largely associated with size and mobility. Large fast forms are less susceptible than small slow forms. Evolutionary adaptation to cave life does not appear to affect this in the absence of food. In the presence of food troglophile species of *Pseudosinella* show a greater susceptibility to predation, than in its absence.

With the exception of spiders, which appear to be much more efficient, predation differences among predators are small. On a basis of this study a sequence of progressively less efficient forms can be made as below : *Scotolemon* > *Neaphanops* > *Aphaenops* > *Lithobius* > *Ameroduvalius* > *Pseudanopthalmus*.

Résumé.

Les espèces de collemboles diffèrent d'une façon frappante quant à leur susceptibilté aux attaques des prédateurs. Les différences dépendent surtout de la taille et de la mobilité. Les formes grandes et rapides y sont moins susceptibles que les formes petites et lentes. L'adaptation évolutive à la vie des cavernes ne semble pas y avoir de l'influence en l'absence de la nourriture. Les espèces troglophiles de *Pseudosinella* font voir en présence de la nourriture, une plus grande susceptibilité aux attaques des prédateurs qu'en l'absence de nourriture.

A l'exception des araignées, qui semblent plus efficaces, les prédateurs diffèrent peu en efficacité. Avec cette étude comme base, on peut établir cette série de formes par ordre d'efficacité décroissante : *Scotolemon* > *Neaphanops* ≃ *Aphaenops* > *Lithobius* > *Ameroduvalius* > *Pseudanopthalmus*.

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